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ECOSPHERE

REPLY

The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka: Reply

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We defined the "perfect mixing paradox" as the counterintuitive theoretical result that when merging separate logistically growing subpopulations, the asymptotic total population size will be different from the sum of the local carrying capacities (Arditi et al. 2016). This phenomenon was demonstrated in a simple model that assumed identical dispersal rates in each patch. In an article published in the present issue of *Ecosphere*, Ramos-Jiliberto and Moisset de Espanés (2017) (RJME) show that this paradox does not occur when assuming balanced dispersal. In our present Reply, we will study a more general dispersal model that encompasses both our original model and RJME's new model. We will show that the perfect mixing paradox is a very common feature of this general model. The additivity of carrying capacities is observed in two special cases only, one of which being RJME's model. In general, carrying capacities do not add up when merging separate subpopulations, even with non-identical dispersal rates.

In Arditi et al. (2016), we considered the following model for logistic growth in two coupled patches:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1N_1\left(1-\frac{N_1}{K_1}\right)+\beta(N_2-N_1),\\ \frac{dN_2}{dt} &= r_2N_2\left(1-\frac{N_2}{K_2}\right)+\beta(N_1-N_2).\end{aligned} \quad (1)$$

We showed that in the case of perfect mixing (i.e., when the migration rate $\beta \to \infty$), the total population N_T follows also a logistic equation with a carrying capacity K_T but does not (in general) equilibrate at the sum of the two carrying capacities $K_1 + K_2$. That is, in general, $K_T \neq K_1 + K_2$: The total population's carrying capacity can either be greater or smaller than $K_1 + K_2$. For example, when the two intrinsic growth rates are equal ($r_1 = r_2$), merging two patches with unequal carrying capacities ($K_1 \neq K_2$) is always detrimental: $K_T < K_1 + K_2$. The opposite inequality is observed when the two intrinsic growth rates are correlated with the local carrying capacities ($r_1 < r_2$ when $K_1 < K_2$): In this case, perfect mixing is always beneficial ($K_T > K_1 + K_2$). When mixing is not perfect (i.e., with finite values of β), it is also a general rule that $K_T \neq K_1 + K_2$, but the direction of the inequality follows more complex conditions (Arditi et al. 2015).

In Eq. 1, we assumed for simplicity that the migration rates were equal in both directions: All individuals in patch 1 and in patch 2 have the same probability of leaving their patch. This is a standard assumption in the eco-mathematical literature and (as recalled by RJME themselves) it has a long tradition in ecological theory, dating back to the 1970s or even earlier. We used it as the "null model" for migration, that is, as the model that can be used until contrary evidence.

Ramos-Jiliberto and Moisset de Espanés (2017) propose the following alternative model:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1N_1\left(1-\frac{N_1}{K_1}\right)+\beta\left(\frac{N_2}{K_2}-\frac{N_1}{K_1}\right),\\ \frac{dN_2}{dt} &= r_2N_2\left(1-\frac{N_2}{K_2}\right)+\beta\left(\frac{N_1}{K_1}-\frac{N_2}{K_2}\right).\end{aligned} \quad (2)$$

The authors show that in this model, the equality $K_T = K_1 + K_2$ is always true. Thus, the model

Citation: Arditi, R., L.-F. Bersier, and R. P. Rohr. 2017. The perfect mixing paradox and the logistic equation: Verhulst vs. Lotka: Reply. Ecosphere 8(7):e01894. 10.1002/ecs2.1894

Received 2 June 2017; accepted 8 June 2017. Corresponding Editor: Debra P. C. Peters.

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does not present the "perfect mixing paradox": There is strict additivity of carrying capacities. This mathematical result is correct.

The fact that changing the model changes the results is not surprising. So, the question is whether the model proposed by RJME is to be preferred over ours. Since RJME do not change the demographic part of the model (logistic growth in each patch), the debate lies in the migration part of the model only. Ramos-Jiliberto and Moisset de Espanés (2017) claim that their model 2 is "slightly more realistic" than model 1 and conclude that the perfect mixing paradox is not a general result. We will reply to this claim in two main points:

1. We will discuss the biological rationale that underlies the migration terms of model 2.
2. We will move beyond the polemical opposition of models 1 and 2 by embedding both of them into a more general model. We will show that the perfect mixing paradox exhibited by model 1 is also a generic property of this more general model.

Balanced dispersal and the ideal free distribution

As explained by RJME, their model 2 is known as the balanced dispersal model proposed by McPeek and Holt (1992). In contrast, our model 1 belongs to the class of source–sink and source–pseudo-sink models. DeAngelis et al. (2016) provide in their introduction an excellent overview of these two classes of dispersal models.

In model 2, the probability of an individual to leave its patch is inversely proportional to the local carrying capacity. It was shown by McPeek and Holt (1992) that this migration rule is related to the ideal free distribution: Whatever the initial distribution, the two subpopulations become rapidly proportional to the local capacities ($N_1/K_1 = N_2/K_2$) and they equilibrate asymptotically at these capacities ($N_1^* = K_1; N_2^* = K_2$). Thus, by definition, we must have $K_T = K_1 + K_2$. The additivity of carrying capacities is built into the model from the outset, and the absence of the perfect mixing paradox is somewhat a tautological consequence. Note that this is also true for any value of the migration rate β , not only with perfect mixing (R. Arditi, C. Lobry, and T. Sari, *unpublished data*).

In model 2, it is assumed that individuals have perfect and instantaneous knowledge of the carrying capacity of their local patch. In contrast, our model 1 assumes that individuals are ignorant and have equal probabilities of leaving their patch, whatever its carrying capacity. Clearly, the "truth" must lie somewhere in-between, which can be formalized in the following model.

A general model with asymmetrical migration

It is easy to formulate a more general model with different migration rates:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left(1-\frac{N_1}{K_1}\right)+\beta_2 N_2-\beta_1 N_1,\\ \frac{dN_2}{dt} &= r_2 N_2\left(1-\frac{N_2}{K_2}\right)+\beta_1 N_1-\beta_2 N_2.\end{aligned} \tag{3}$$

Here, β_1 is the per capita migration rate from patch 1 to patch 2 and β_2 the rate from patch 2 to patch 1. Model 3 is of a higher dimension than models 1 and 2 (one more parameter), and its mathematical properties will be less specific. However, we will show below that *in general*, it remains true that $K_T \neq K_1 + K_2$.

Our model 1 is the special case of model 3 with $\beta_1 = \beta_2$. Ramos-Jiliberto and Moisset de Espanés (2017)'s model 2 is the special case with:

$$\beta_1 = \frac{\beta}{K_1},\ \beta_2 = \frac{\beta}{K_2}, \text{or, in other terms,}\ \ \frac{\beta_1}{\beta_2} = \frac{K_2}{K_1}. \tag{4}$$

We can reformulate the general model 3 as:

$$\begin{aligned}\frac{dN_1}{dt} &= r_1 N_1\left(1-\frac{N_1}{K_1}\right)+\beta\left(\frac{N_2}{\gamma_2}-\frac{N_1}{\gamma_1}\right),\\ \frac{dN_2}{dt} &= r_2 N_2\left(1-\frac{N_2}{K_2}\right)+\beta\left(\frac{N_1}{\gamma_1}-\frac{N_2}{\gamma_2}\right).\end{aligned} \tag{5}$$

Thus, by definition, $\beta_i = \beta/\gamma_i$. With the assumption $\gamma_1 = \gamma_2 = 1$, this model is identical to our model 1, and with the assumption $\gamma_1 = K_1$, $\gamma_2 = K_2$, it is identical to RJME's model 2. (Strictly speaking, model 5 is overparameterized. The independent parameters of the migration submodel are β and γ_1/γ_2, and RJME's model is obtained with $\gamma_1/\gamma_2 = K_1/K_2$.)

Using the methods explained in the appendices of Arditi et al. (2016) and in the present Appendix S1, it is easy to show that under perfect mixing ($\beta \to \infty$), model 5 predicts (from A1)

$$\frac{N_1}{\gamma_1} = \frac{N_2}{\gamma_2}$$

and (rewriting A2 to isolate $K_1 + K_2$)

$$K_T = (K_1 + K_2) + \frac{r_1\left(1 - \frac{\gamma_1 K_2}{\gamma_2 K_1}\right) + r_2\left(1 - \frac{\gamma_2 K_1}{\gamma_1 K_2}\right)}{r_1 \frac{\gamma_1}{\gamma_2 K_1} + r_2 \frac{\gamma_2}{\gamma_1 K_2}}. \quad (6)$$

Eq. 6 shows that in general, $K_T \neq K_1 + K_2$. Therefore, the perfect mixing paradox is observed in model 5, as this was the case in our original model 1. If we assume (with no loss of generality) that $K_1 > K_2$, Expression 6 can be represented graphically as a function of $x = \gamma_1/\gamma_2 = \beta_2/\beta_1$ (Fig. 1). This figure shows that for intermediate values of x, perfect mixing is beneficial ($K_T > K_1 + K_2$), while it is detrimental for low and high values. Strict additivity (i.e., $K_T = K_1 + K_2$) occurs only when the numerator of the large fraction in Eq. 6 is zero. We show in Appendix S1 that this happens in the two special cases (A5 and A6) corresponding to the two special points in Fig. 1.

The first case (full symbol in Fig. 1) is $\gamma_1/\gamma_2 = K_1/K_2$, or $\beta_1 = \beta/K_1$, $\beta_2 = \beta/K_2$, which characterizes RJME's model 2. Thus, although our model 1 and RJME's model 2 have the same number of parameters, ours is a "generic" representative of the more general model 5 while RJME's model is a special case, corresponding to a singular situation in parameter space. The second case (open symbol in Fig. 1) for which the numerator in model 6 is zero is $\gamma_1/\gamma_2 = \alpha_2/\alpha_1$, or $\beta_1 = \beta\alpha_1$, $\beta_2 = \beta\alpha_2$. This is another singular situation in parameter space. In more biological terms, the first case is balanced dispersal (dispersal β_i inversely proportional to carrying capacity K_i). The second case occurs when dispersal is proportional to the intraspecific competition parameter α_i. Incidentally, this is another example that shows the advantage of Verhulst's formalism over Lotka's (see Arditi et al. 2016).

In conclusion, RJME's article has the merit of raising interesting questions about the underlying paradigm of the migration model. Their balanced dispersal model requires that individuals have instantaneous and perfect knowledge of the patch richness, which is a very strong behavioral assumption. The more general model that we propose in the present paper shows that the perfect mixing paradox defined in Arditi et al. (2016) occurs in much wider conditions than those originally considered. We have clarified the two very special cases under which the perfect mixing paradox does not occur, one of which being specific to RJME's model that assumes balanced dispersal.

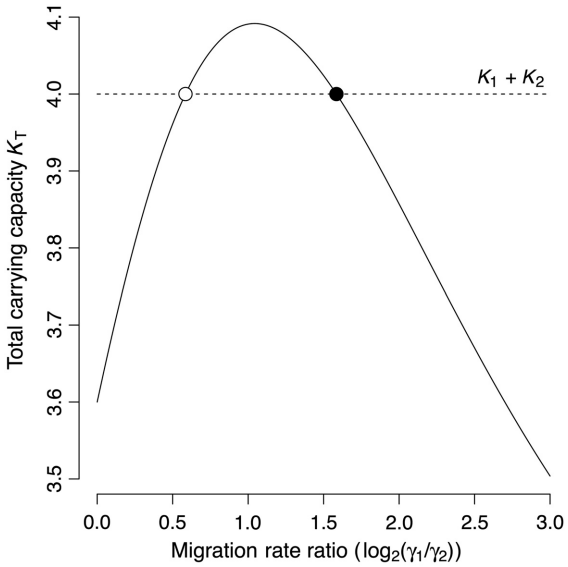

Fig. 1. Graphical representation of Eq. 6 illustrating the perfect mixing paradox. In general, the total carrying capacity is either higher or lower than the sum of the two patches' capacities. Equality ($K_T = K_1 + K_2$) occurs in two special cases only. Ramos-Jiliberto and Moisset de Espanés (2017)'s model corresponds to the full black point, showing that this model is not a representative of the general case (values used in this figure for illustrative purpose: $r_1 = 2$, $r_2 = 1$, $K_1 = 3$, $K_2 = 1$).

Acknowledgments

This work received funding from the Swiss National Science Foundation (grant 31003A_165800/1 to LFB).

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.1894/full